SOME ABNORMAL INFLORESCENCES

A. M. Johnson

Ceratonia Siliqua L.

The carob or St. John's bread, *Ceratonia Siliqua* L., is a common ornamental in southern California. It is indigenous to the Mediterranean region, where it may grow to a height of fifty feet. Normally, the flowers are polygamo-dioecious and are borne in racemes. Petals are wanting. At the base of the gynoecium is a prominent gland (pl. 15, B, *gl*). The carpels, as they grow to maturity, become more or less strongly curved.

The abnormal inflorescences here to be described were found in November, 1934, by my colleague, Dr. Carl Epling, who kindly turned them over to me for study. There were nine inflorescences, all of them carpellate. One of the peculiar features of these inflorescences (except one) was that the gynoecium of the terminal (uppermost) flower consisted of more than one carpel—the number of carpels ranging from two to four. A four-carpellate gynoecium was present in two instances; in five instances the gynoecium was three-carpellate, and in one instance, two-carpellate (pl. 15, A, B).

The remaining inflorescence differed markedly from those above mentioned in that the gynoecium of the terminal flower was replaced by an elongate axis bearing sixteen carpels, the four lowest of which formed a basal whorl, while the other twelve were spirally arranged along the axis (pl. 15, E). The four basal carpels were adnate by their stipes (gynophores) to this (central) axis. Between the four terminal carpels there were two minute rudimentary ones (pl. 15, F). Although these carpel rudiments appear to be apical in relation to the axis, it is probably correct to assume that they are morphologically lateral, as are the other carpels on the axis.

In outward appearance this carpel-bearing axis bore a marked resemblance to a normal inflorescence. However, none of the twelve spirally arranged carpels showed any indication of arising from an individual stipe—that is, they were all sessile. The only indication of such a stipe was below the basal whorl of four carpels. Nor was there any indication of the presence of the gland so characteristic of normal flowers. These distinctions will be seen clearly in the accompanying figures. Aside from these details and the fact that these carpels were smaller and that some of them were not completely closed (pl. 15, G, H, J) they had the appearance of normal carpels.

The illustrations (pl. 15, B, C, D, G, I, J) show that the common stipe varied somewhat in length: in figures C, D, and G it is relatively long; in B, I, and J it is shorter. Thus the situation

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under discussion (pl. 15, E) may be regarded as an exaggerated state of figure G, for example—indeed, the presence of the rudimentary carpels at the summit of G suggests that had the development proceeded further there might have resulted a state comparable to that at E. The same argument applies to the other similar cases illustrated (pl. 15, I, J).

It seems obvious, therefore, that we have here not a proliferation, so to say, of the primary inflorescence, but rather a pluricarpellate (pleiomerous) condition of the gynoecium of the terminal (but not morphologically apical) flower, in which the common stipe or gynophore of the several carpels has developed as an elongate axis, making the whole appear as though it were a secondary inflorescence.

Rudimentary "apical" carpels were found in a few instances, but not all on the same inflorescence. Two of these instances are figured (pl. 15, G, H, J). For comparison with the abnormal states the terminal portion of a normal inflorescence is figured (pl. 15, K). Here the carpels of three normal flowers are shown. The difference between this state and that of the abnormal ones is striking.

Quercus agrifolia Neé

The inflorescences of the coast live oak, *Quercus agrifolia* Neé, were borne on the lower portion of a shoot of the season (pl. 16, A, *a, b, c*). There were three inflorescences, the lowest, and shortest (*a*), consisted of nine flowers, of which the second and the two terminal ones had been broken off; the second and longest inflorescence (*b*) bore eleven flowers; the third and next longest (*c*) bore nine flowers. In all three inflorescences, as will be seen from the figures, the flowers were grouped in pairs, the pairs more or less closely approximate along the upper portion of the inflorescence, while the few lower flowers were solitary and more or less remote.

The morphological nature of the flowers of the three inflorescences is schematically represented in text figure 1. As will be

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Explanation of the Figures. Plate 15.

Plate 15. Ceratonia Siliqua: apical portion of six inflorescences. A, terminal gynoecium of 2 distinct carpels arising from same stipe (gynophore), *gl,* gland. B, terminal carpels of A enlarged. C, terminal 3-carpellate gynoecium. D, terminal carpels of C enlarged; carpel *a* separate from carpels *b* and *c* except at base of common stipe. E, gynoecium of terminal flower replaced by elongated axis bearing 16 carpels, the 4 lowest whorled, 12 above spirally arranged. F, apical carpels of E with 2 rudimentary carpels between them. G, terminal 4-carpellate gynoecium arising from a common stipe: *c,* calyx, *br,* minute bracts, *x,* smallest carpel, open at base exposing an ovule. H, carpel *x* of G; *ov,* exposed ovule, *n,* rudimentary carpels. I, terminal gynoecium of 3 carpels arising from a common stipe. J, opposite side of terminal gynoecium of I showing smallest carpel open at base exposing an ovule and 2 rudimentary carpels in front of ovule. K, normal inflorescence showing 3 normal carpels developed from 3 flowers.

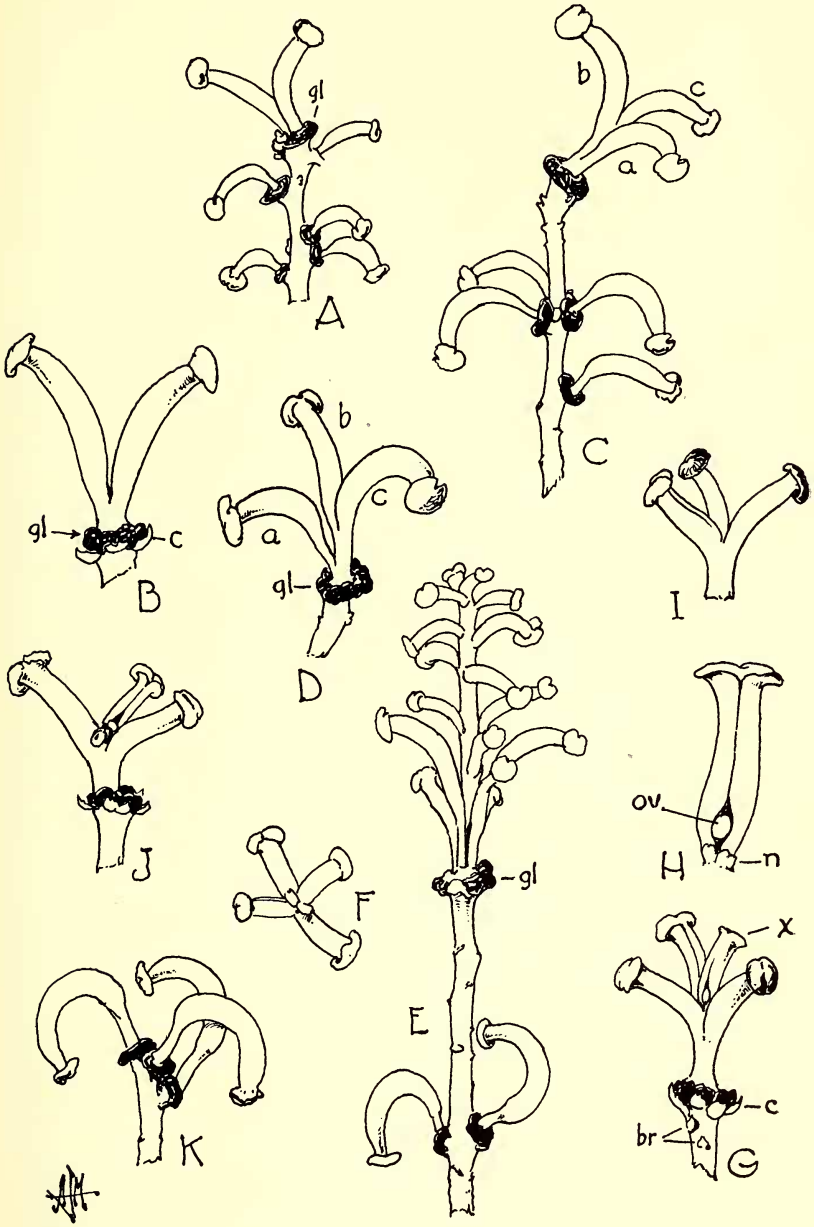

PLATE 15. CERATONIA SILIQUA: APICAL PORTION OF SIX INFLORESCENCES.

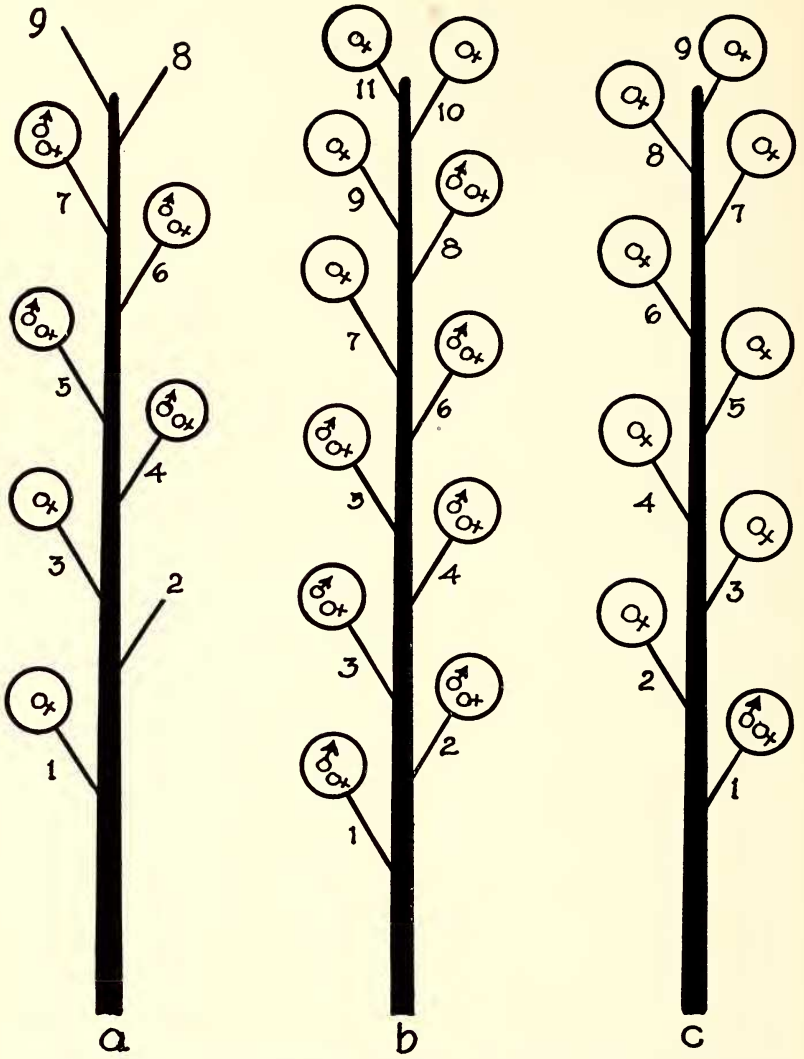

FIG. 1. *Quercus agrifolia* Neé. Diagrammatic representation of inflorescences *a*, *b*, *c* (pl. 15, A). Carpellate and bisexual flowers are designated by conventional symbols.

seen from the first diagram (*a*) two of the lower flowers (1, 3) were carpellate, while the four next above (4, 5, 6, 7) were bisexual; the missing flowers are represented by the numerals 2, 8, and 9. In the next and longest inflorescence (*b*) all but four of the eleven flowers were bisexual, the four exceptions (7, 9, 10, 11) being carpellate. In the third inflorescence (*c*) only a single flower, the lowermost of the nine, was bisexual, all the others being carpellate.

In text figure 2 are shown the floral diagrams of the seven bisexual flowers (1, 2, 3, 4, 5, 6, 8) of inflorescence *b*. These empirical diagrams show the orientation of the styles (shaded black) in relation to the stamens and the perianth segments. In these as in all the other flowers examined (pl. 16) it will be seen that there is a marked variation in the number of stamens and of styles present. Certain modifications of the individual organs will also be noted. The number of normal styles ranged from two to four. In flower 3 (text fig. 2) one of the stamens (shown at the left in the diagram) was a mere rudiment; in flowers 4 and 6 one of the styles was staminodial along one side, and each bore an anther; in flower 8 only a single stamen was present, along with four styles; in one of the two stamens in flower 5 one of the anther sacs was rudimentary.

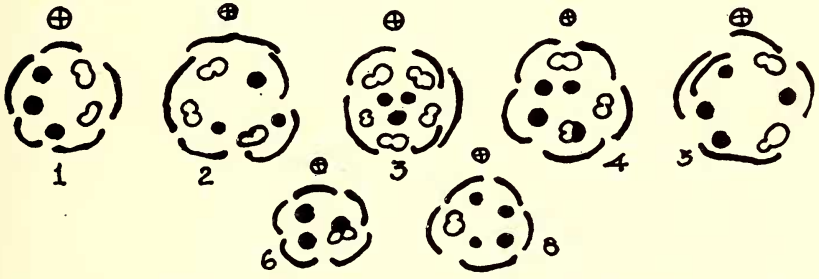

Fig. 2. *Quercus agrifolia* Neé. Empirical diagrams of flowers 1, 2, 3, 4, 5, 6, 8, inflorescence *b*.

Some rather pronounced variations and modifications were found in the flowers of inflorescence *a*. The floral diagrams (styles shaded black) of five of these flowers are figured (pl. 16, J, K, L, M). As in flowers 4 and 6 of inflorescence *b* we find here also, in the lowermost flower, a half-staminodial style bearing an anther on the modified side (pl. 16, J). This anther-bearing style and two of the other styles present differed from the normal fourth style in being very slender, yet of the same length as the normal style. Besides these peculiarities there was present, closely approximate to the base of the anther-bearing style, a minute rudimentary organ which, from its appearance, could be interpreted as a fifth style (pl. 16, E, *x*). The anther sacs of the adjacent staminodial styles were of unequal size, elongate, and pointed at the ends (pl. 16, F). In the fourth flower of this inflorescence (*a*) four normal stamens were present, along with three dissimilar styles—one normal, the other two very slender and with somewhat abnormal stigmas (pl. 16, G, K); the stamens were all normal. In the fifth flower there were five normal stamens and three abnormal styles which were more or less coalescent basally. The sixth flower showed one normal stamen, one stamen with a normal anther but with a short modified filament which

was coalescent basally with the base of the adjacent style, and besides these a smaller stamen with an abnormal anther, and one rudimentary stamen (*r*). Two of the three styles in this flower were very stout and strongly bent at the middle, the larger of the two otherwise having a normal appearance; the third style was minute and abnormal. All three styles were coalescent at the base (pl. 16, I, M). Stout styles of the geniculate shape just mentioned were found in a few other flowers as well. In the seventh flower there were two normal stamens and three apparently normal styles which were coalescent at the base (pl. 16, N).

In inflorescence *c* the lowermost flower (1) appeared to be normal in every respect. This was the only flower of the entire lot from the three inflorescences which did not show any detectable abnormality in the organs present.

A strongly geniculate condition was found in the three styles of the third flower on inflorescence *b*, except that in this case the styles were more slender and, as far as could be discerned, all were normal (pl. 16, C, D).

As will be seen from the floral diagrams in plate 16 and in text figure 2, the orientation of the floral organs in relation to the median and the transverse planes of the flowers is very erratic. In the normal flower (1) of inflorescence *c* (pl. 16, B) three stamens are situated anteriorly, the middle one of which lies in the median plane opposite a posterior median style. The reverse of this situation is seen in the fourth flower of inflorescence *a*: two of the three styles lie posteriorly in a transverse plane, while the third style lies anteriorly in the median plane (pl. 16, K). A similar situation obtains in flower 3 of inflorescence *b* (text fig. 2). A fairly evenly whorled arrangement of the stamens and styles was found in a number of instances (pl. 16, J; text fig. 2, flowers 1, 2, 5, 8). As regards the ovaries these appeared to be as well developed as in normal carpellate flowers (pl. 16, B, C. D, E).

In retrospect it will be noted that in the three inflorescences the majority of the flowers (present) of inflorescence *a* were bisexual, or in the ratio of four to two; in inflorescence *b* the ratio was seven to four; in *c* it was one to eight. In other words the total number of bisexual flowers in proportion to unisexual (carpellate) flowers was twelve to thirteen—that is, a nearly equal distribution. No staminate flowers were found. In only one flower (bisexual) were the organs present normal in every respect. Three flowers had modified (staminodial) styles bearing

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Explanation of the Figures. Plate 16 (*continued from page 183*).

I, flower 6, anterior view, showing two strongly geniculate styles and a third rudimentary style immediately to the left; *p*, perianth; *t*, stamens; *r*, rudimentary stamen. J–N, empirical diagrams of flowers in inflorescence *a* (in L, M and N coalescence of styles is indicated by black lines): J, flower 1 (see also E). K, flower 4. L, flower 5. M, flower 6, styles coalesced with a stamen (see also I). N, flower 7.

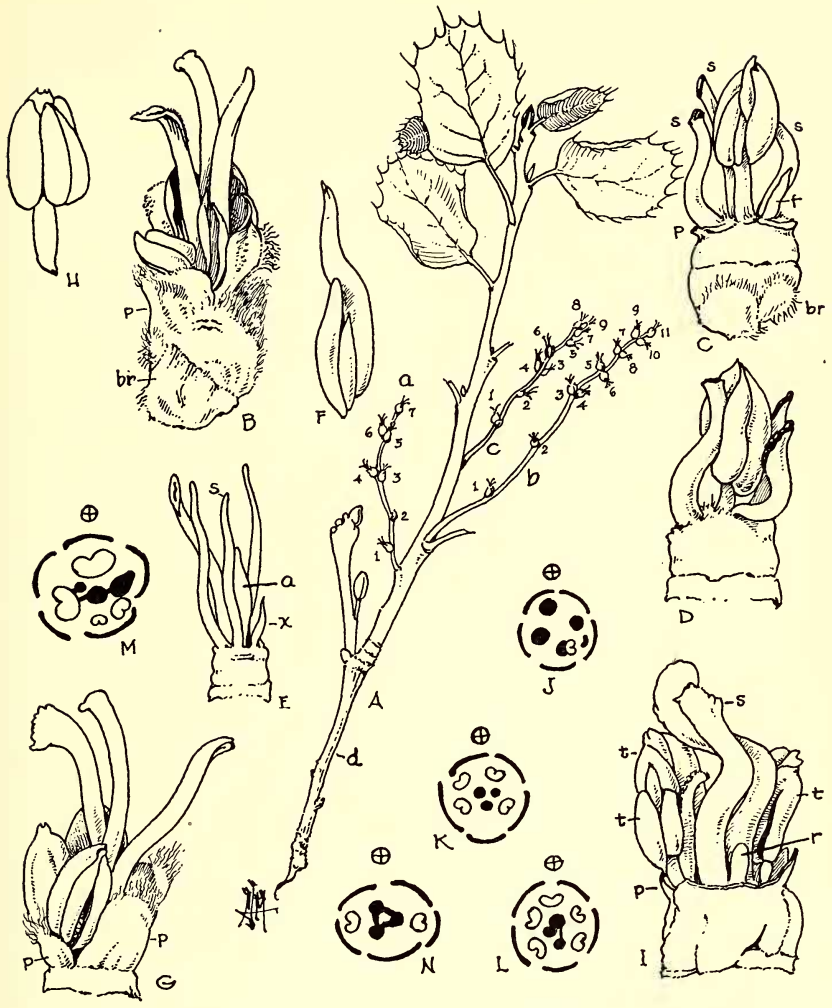

Plate 16. Abnormal inflorescences of Quercus agrifolia Neé. A, shoot: *a, b, c,* abnormal inflorescences; *d,* growth of previous season. B, flower 1, inflorescence *c*: showing three styles and five stamens (three in full view); *br,* basal bract folded back; *p,* perianth. C, flower 3, inflorescence *b,* adaxial side with perianth removed: *br,* minute bracts; *p,* base of the removed perianth; *s,* styles; *f,* filament of a second stamen—at its left a stamen with one anther-sac abnormal. D, flower 3, inflorescence *b,* showing strongly geniculate styles. E–I, detail of flowers from inflorescence *a*: E, flower 1, normal style (at left); two filamentous abnormal styles; *s,* filamentous abnormal staminodial style bearing abnormal anther *a* on one side; *x,* rudimentary style. F, dorsal aspect of the anther-bearing style in E, showing the abnormal and unequal anther sacs. G, flower 4, anterior view, showing three dissimilar styles and three of the four stamens; *p,* perianth. H, one of stamens shown in G. (*Continued on page 182.*)

an anther on the staminodial side. The stamens present ranged in number from one to five and the styles from two to four. In no case were the perianth segments modified in any way.

Department of Botany,
University of California at Los Angeles,
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CYTOPHYLETIC ANALYSIS OF CERTAIN ANNUAL AND BIENNIAL CRASSULACEAE

J. T. Baldwin, Jr.

An attempt is here made to analyze from a cytophyletic viewpoint the relationship existent among several annual and biennial Crassulaceae, a family predominantly perennial. Such an analysis necessarily passes from fact to hypothesis, but the analysis should be made. Observations isolated have restricted meaning; from them integrated, hypotheses may be formulated and, with the accumulation of evidence, may be re-examined and tested.

The systematic history of certain of the species considered is a record of many taxonomic maneuvers. That history is reviewed. Each different taxonomic concept of a plant should be indicative of that plant's affinities. The plants treated here will doubtless be subjected to other changes in nomenclature. And that is as it should be. "There is no finality in taxonomy" (L. H. Bailey).

Sedum pusillum Michx.

Michaux (20, 1803) described as *Sedum pusillum,* a small, octandrous, white-flowered plant from Flat-rock, North Carolina. Pursh (22, 1814), apparently confusing Michaux's species with the plant later designated *S. Nevii* Gray, reported *S. pusillum* to be perennial and to occur in Virginia "on the east banks of the Shanadoah River." Nuttall (21, pp. 110, 293, 1818) included *S. pusillum* as a synonym of his *Tillaea ? cymosa* and (21, p. 293) made both *Tillaea ? cymosa* and *Sedum pusillum* synonymous with *Diamorpha pusilla.* Gray (17, 1876) first recognized that Nuttall and subsequent writers had confounded two species and that *Sedum pusillum* and *Diamorpha pusilla* are distinct. Gray, in 1875, found them both in great abundance on Stone Mountain in Georgia; Canby had collected the two there in 1869 but had not differentiated between them. Rose (24, 1905) established for Michaux's species the monotypic genus *Tetrorum;* Berger (6, 1930) and Fröderström (16, 1935) again referred the plant to *Sedum.* The species is known only from North Carolina and Georgia. As treated by Fröderström, the species has narrowly spurred leaves, 4- to 5-parted flowers with white or purple petals broad at the base, immature carpels suberect and broad-styled,